

## 2.

A Study of the Anoplocephaline Cestodes of  
North American Rabbits.<sup>1</sup>

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(Text-figures 1-23).

## 1. INTRODUCTION.

Previous work on the anoplocephaline cestodes of North American rabbits has resulted in much confusion. Observations on internal anatomy, time of appearance of genital primordia, number of testes and other morphological details are so lacking in agreement that any interpretation is difficult. Baer (1927) and Sprehn (1932) have incorrectly cast all American leporine species of the genus *Cittotaenia* into synonymy with the European species *C. pectinata* (Goeze, 1782). The purpose of the present investigation was to secure precise information on the North American representatives of this genus, correct the errors, and eliminate the confusion that has existed in the knowledge of the rabbit cestodes of the family Anoplocephalidae.

## 2. ACKNOWLEDGEMENTS.

The present study was suggested by Professor Horace W. Stunkard and carried out under his direction. The author wishes to thank Professor Stunkard for helpful criticisms, for the loan of the European material used in comparison, and for the use of his private library. Grateful acknowledgement is also extended to Dr. Maurice C. Hall, U. S. Bureau of Animal Industry, U. S. Department of Agriculture, for the privilege of studying original material deposited in his care. The kindness of Dr. R. V. Boughton of the University of Manitoba, in lending specimens of *Cittotaenia pectinata americana*, is recognized. Lastly, the author gratefully acknowledges the assistance of Marion E. Arnold for criticisms and aid in the preparation of this paper.

## 3. MATERIALS AND METHODS.

The material used in this study consisted of both North American and European species. Specimens of all the American species and four of the five European ones provided material for a comprehensive treatment of the subject. *Andrya rhopalocephala* from European hares is rare and no material of that species was available. Since doubt has been expressed con-

<sup>1</sup> Contribution from the Biological Laboratory, New York University, University Heights, New York.

cerning the specific distinctness of the North American species, a detailed comparison has been made between North American and European forms.

Specimens of *Cittotaenia denticulata* (Rudolphi, 1804), *C. etenoides* (Railliet, 1890), *C. pectinata* (Goeze, 1782), and *Andrya cuniculi* (Blanchard, 1891) were loaned to the writer by Professor Stunkard, who collected them during 1931 and 1932 from the vicinity of Hamburg, Germany.

The American specimens of the family Anoplocephalidae were obtained from various sources. The writer examined the intestines of 9 cottontail rabbits, *Sylvilagus floridanus mallurus*, killed near New York City; 7 of the same species from Boylesville, Pennsylvania; 7 from cottontails killed in northern New York State; and 156 from cottontails, *Sylvilagus floridanus alacer*, killed near Wichita, Kansas. The material in the last two groups was obtained from slaughter houses in New York City. All the parasites were killed and fixed in a saturated solution of corrosive sublimate and were washed, stained, dehydrated, cleared, mounted and studied either as sections or *in toto*. Alcoholic and mounted specimens of the genera *Cittotaenia* and *Schizotaenia* were secured through the kindness of Dr. M. C. Hall. Similar specimens of *C. pectinata americana* were loaned by Dr. R. V. Boughton.

#### 4. HISTORICAL REVIEW.

The subfamily Anoplocephalinae was erected by Blanchard (1891), and the family Anoplocephalidae by Kholodkovsky (1902). Fuhrmann (1907) characterized the family Anoplocephalidae as follows: "Scolex meist kugelig, seltener gestreckt, unbewaffnet; Saugnäpfe verhältnismässig gross; Hals fehlt; Glieder kurz und breit; Genitalien einfach oder doppelt. Genitalpori randständig; Eier oft mit einem 'birnförmigen Apparat.' In Säugetieren und Vögeln." In his recent monograph, Fuhrmann (1931) gave a more extended diagnosis of the family. He stated: "Scolex immer ohne Rostellum. Glieder meist breiter als lang. 1 oder 2 Genitalapparate in einer Proglottis. Genitalöffnung beidseitig, einseitig, regelmässig oder unregelmässig alterierend. Weibliche Genitalöffnung oft verschwindend, selten fehlend. Hoden zahlreich. Weibliche Geschlechtsdrüsen häufig poral verschoben. Uterus sackförmig, retikulär oder sich in Ei-Kapseln auflösend oder mit 1 bis zahlreichen Paruterinorganen versehen. Eier mit 3 Hüllen, von welchen die innerste oft einen birnförmigen Apparat aufweist. Entwicklungsgeschichte vollständig unbekannt. In Reptilien (2 Genera), in Vögeln (7 Genera), in Säugern (21 Genera)."

Five species of anoplocephaline cestodes occur in European hares and rabbits. Three of them belong to the genus *Cittotaenia*, the others to the genus *Andrya*. The American leporine cestodes belong to the genera *Cittotaenia* and *Schizotaenia*. Although the genus *Andrya* is represented in North America, species have not yet been found in rabbits and hares. To facilitate description and avoid repetition, the diagnostic features of the three genera are listed.

*Andrya* Railliet, 1893, Anoplocephalinae: Segments much broader than long except in most distal parts of strobila. Single set of reproductive organs in each segment; genital pores irregularly alternate. Testes mostly on aporal side of segment; female genitalia on poral side. Uterus typically reticular to saccular. Pyriform apparatus present. Adults in mammals.

*Type species:* *A. rhopalocephala* (Riehm, 1881).

*Cittotaenia* Riehm, 1881. Anoplocephalinae: Segments broader than long. Double set of reproductive organs in each proglottid; genital pores in each lateral wall. Uterus saccular. Pyriform apparatus present. Adults in mammals and birds.

*Type species:* *C. denticulata* (Rudolphi, 1804) Stiles, 1896.

*Schizotaenia*, Janicki, 1906. Anoplocephalinae: Segments much broader

than long. Single set of reproductive organs to each segment; genital pores typically alternate. Testes in median field or segment; female genitalia slightly to aporal side. Uterus reticular. No pyriform apparatus present. Adults in mammals.

*Type species: S. decrescens* (Diesing, 1856).

A brief historical account of each species considered in the present paper is given later with the specific description. For more detailed historical data, the reader is referred to the original sources cited in the bibliography.

##### 5. ANOPLOCEPHALINE CESTODES FROM NORTH AMERICAN HARES AND RABBITS.

Anoplocephaline cestodes were first reported in North American rabbits by Curtice (1888), who described supposedly the early larval stages of *Taenia pectinata* in *Lepus sylvaticus*.

At present, four species of anoplocephaline tapeworms are recognized in North American hares and rabbits: (1) *Schizotaenia americana* (Stiles, 1895) (= *Andrya americana* = *Andrya americana leporis* = *Bertia americana* = *Bertia americana leporis* = *Schizotaenia americana leporis*); (2) *Cittotaenia perplexa* (Stiles, 1895) (= *Ctenotaenia perplexa* = *Cittotaenia mosaica*); (3) *Cittotaenia pectinata americana* Douthitt, 1915 (= *Cittotaenia pectinata* of Lyman, 1902); (4) *Cittotaenia variabilis* (Stiles, 1895) (= *Ctenotaenia variabilis* = *Cittotaenia variabilis variabilis* = *Cittotaenia variabilis angusta* = *Cittotaenia variabilis imbricata*).

#### ***Schizotaenia americana* (Stiles, 1895) Janicki, 1906.**

(Text-figs. 1, 10).

This cestode was first described as *Andrya americana leporis* by Stiles (1895), and was transferred by him (1896) to the genus *Bertia* on the basis of its resemblance to *Bertia americana* (Stiles, 1895). Stiles, 1896, from the porcupine. Stiles postulated that *B. americana leporis* might eventually be elevated to specific rank, but that his five poorly preserved specimens did not warrant such a step. The material was collected by C. Curtice from *Lepus* sp. and the locality in the United States from which it was taken is unknown. Stiles and Hassall (1902) proposed the name *Bertiella* for *Bertia*, since the latter was preoccupied.

Cohn (1906) stated that *Bertia americana* was synonymous with *Taenia laticephala* Leidy. He retained the genus *Bertia* (he had apparently not seen Stiles' and Hassall's new allocation of the species), but placed the specific name, *americana*, in synonymy.

In his description of the cestodes of mammals, Janicki (1906) erected the new genus *Schizotaenia* with *S. macrorhyncha* (Rudolphi, 1810) as type and in it he included *Bertia americana* (Stiles, 1895) and *Bertia americana leporis* (Stiles, 1895).

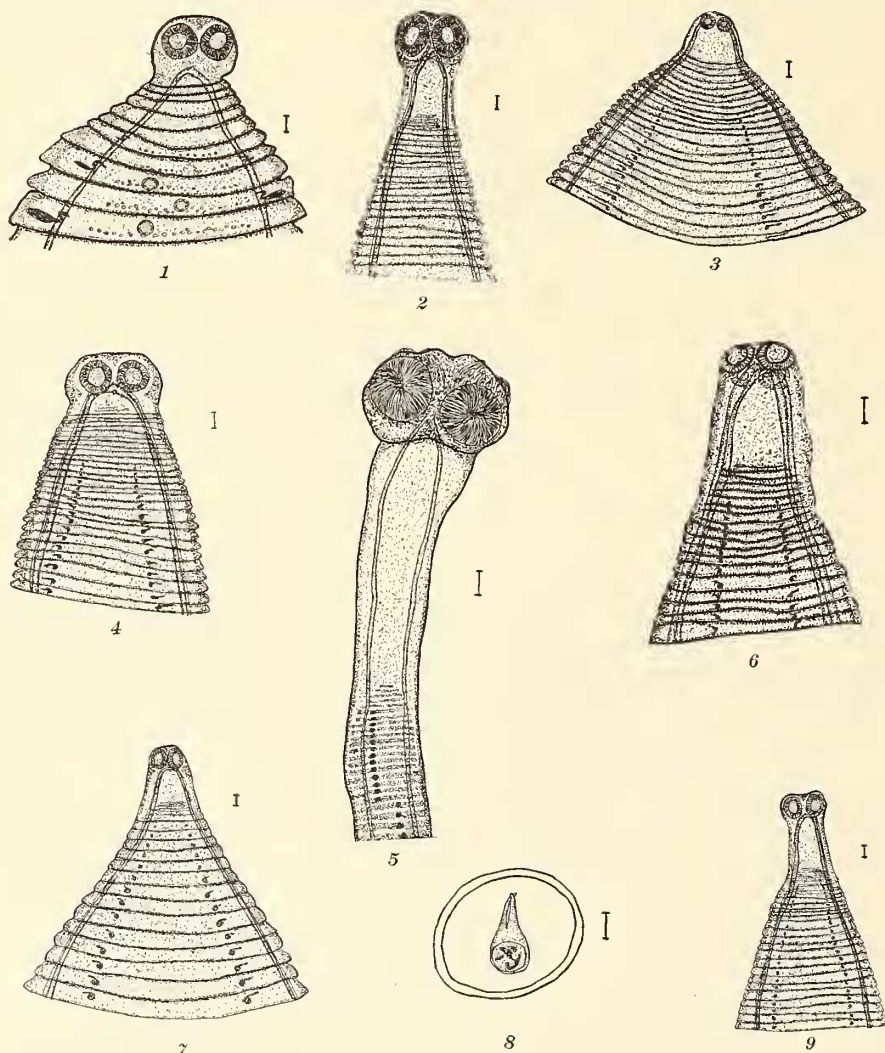
Douthitt (1915) declared that the variety *Schizotaenia americana leporis* (Stiles, 1895) should be dropped in favor of *Schizotaenia americana*. He stated that the variety was too little known and too incompletely described to permit any distinction from *S. americana*. Douthitt gave sound and logical arguments to disprove Cohn's suggestion that *Bertia americana* and *Taenia laticephala* Leidy were identical.

Meggitt (1924) reestablished *Schizotaenia americana leporis* as a valid species. He reduced the species *S. americana*, which is from the porcupine, to synonymy with *S. laticephala*. In this he followed Cohn's contention and disregarded Douthitt's argument.



Baer (1927) removed *Schizotaenia americana* from synonymy with *S. laticephala*. Since he did not mention *S. americana leporis*, he apparently followed Douthitt and considered the leporine variety identical with the porcupine species.

Sprehn (1932), in his *Lehrbuch der Helminthologie*, did not even men-



Text-figures 1-9.

Abbreviations: c—cirrus sac. e—excretory duct. n—nerve fiber. o—ovary. p—pars prostatica. r—seminal receptacle. s—shell gland. t—testis. u—uterus. v—vitelline gland. va—vagina. vd—vas deferens. vs—seminal vesicle. All measurements are to a scale of 0.1 mm., with the exception of Text-figure 8 in which the scale is 0.01 mm. All drawings are camera lucida.

1. Scolex, *Schizotaenia americana*. 2. Scolex, *Cittotaenia variabilis*. 3. Scolex, *Cittotaenia perplexa*. 4. Scolex, *Cittotaenia denticulata*. 5. Scolex, *Andrya cuniculi*. 6. Scolex, *Cittotaenia pectinata americana*. 7. Scolex, *Cittotaenia pectinata*. 8. Ovum, *Cittotaenia denticulata*. 9. Scolex, *Cittotaenia ctenoides*.



tion the genus *Schizotaenia*, or give Janicki as a reference. He also failed to mention either *Bertiella americana* or *B. americana leporis*, although he recognized the generic name, *Bertiella*, proposed by Stiles and Hassall (1902).

The writer was fortunate to obtain a cotype of Stiles' original material of *Schizotaenia americana leporis* (U. S. Nat. Mus. 1170).

Since the specimen was incomplete and in poor condition, the total length and number of proglottids could not be determined. The fragment, consisting of 75 proglottids, measured 33 mm. in length and 6.5 mm. in maximal width. A neck, if present, was too contracted to be recognizable. The scolex (Text-fig. 1) was 0.63 mm. wide (Stiles found it to be 0.64 mm.) and the suckers measured 0.25-0.26 mm. in length and 0.21-0.25 mm. in width. This is a wider variation than found previously in either *Schizotaenia americana* or its variety, *S. americana leporis*.

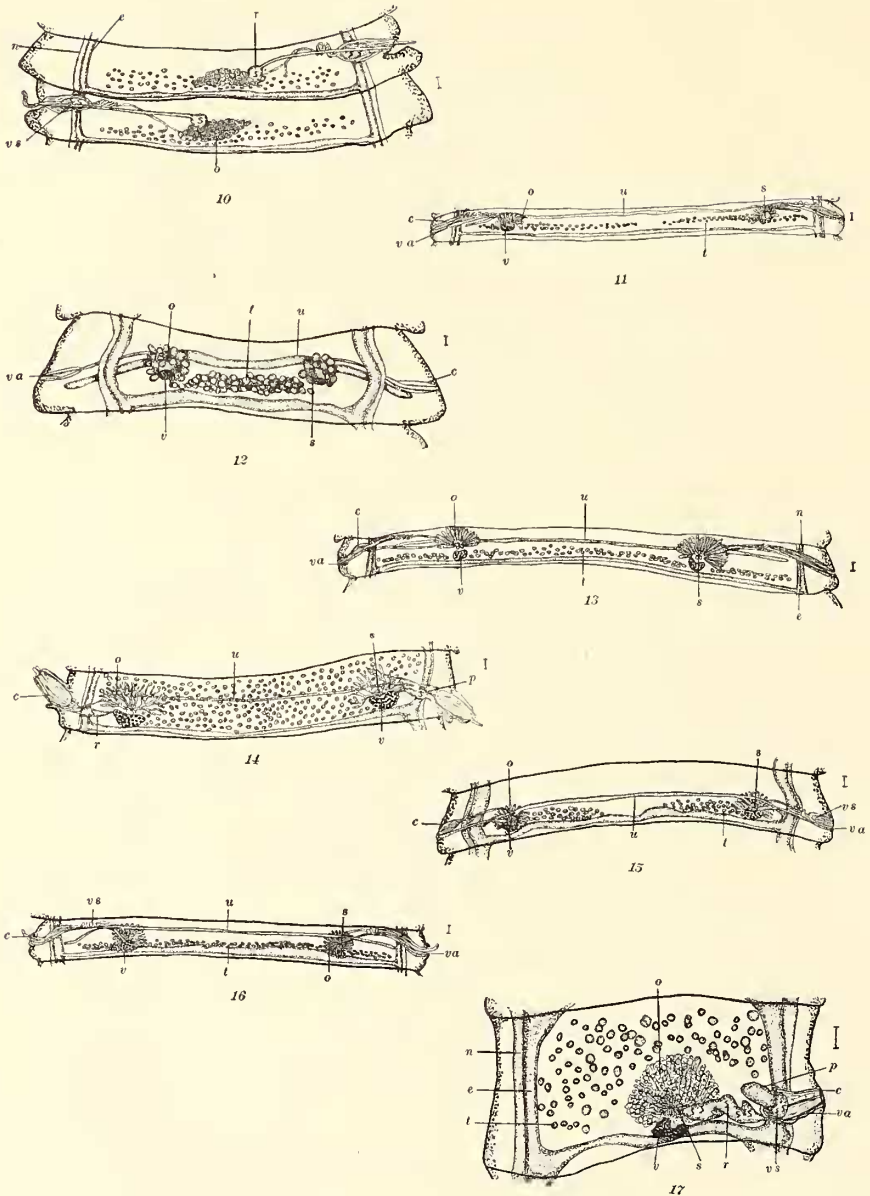
The male genital primordia with evidences of the male ducts appeared first in the sixth proglottid. The cirrus and cirrus sac were well developed by the 20th segment, and the cirrus was seen extruded in the 23rd. Douthitt stated that the genital primordia were present in the first segment. According to Douthitt, sexual maturity was attained in the 80th proglottid (Text-fig. 10). The cirrus sac, containing the seminal vesicle and a long thin cirrus, was very muscular, especially at its proximal end. It measured as much as 0.69 mm. in length. It was Douthitt's opinion that part of the seminal vesicle was outside the cirrus sac. In one of the best preserved proglottids, 65-70 testes (Stiles reported 50) were observed in an irregular row in the distal half of the proglottid. The convoluted vas deferens extended from the region of the ovary to the cirrus sac and, just before it entered the latter, it was surrounded by glandular cells, probably the pars prostatica. The cirrus sac opened to the exterior at approximately the middle of the lateral margin. The vagina emptied just below the male opening. There were indications of a genital papilla.

The primordium of the seminal receptacle first appeared definitely in the eighth segment, although indications were seen in the seventh proglottid. The structure present was rather spherical and was found alternately to the right and left of the median line. The details of the female reproductive system could not be made out. Only two ovaries were measured and their probable widths were 0.53 and 0.63 mm.; Douthitt's measurement of the ovary width was 1.3 mm. The uterus arose from the female genital complex as a fan-shaped structure, and was filled with eggs by the 58th segment. The ova measured 30-40  $\mu$  in diameter, with an average of 39  $\mu$ . According to Douthitt, the outer embryonic membrane ranges from 55-61  $\mu$  in diameter.

Comparison of the specific diagnoses (Stiles, 1896) of *Bertia americana* and *B. americana leporis* disclosed only minor differences which may be regarded as individual variations rather than specific characters. After examination of specimens of *S. americana leporis*, the writer agrees with Douthitt and Baer that the variety name should be suppressed.

From the above description and from a historical review, the following specific diagnosis may be derived.

*Diagnosis: Schizotaenia americana* (Stiles, 1895) Janicki, 1906. Strobilae from 23-47 mm. in length, and from 5-6.5 mm. in maximal breadth. Number of proglottids may exceed 95. Scolex varies from 0.6-0.7 mm. in breadth. Neck absent, strobilization beginning immediately. Genital organs single; pores lateral and regularly alternate. Male genital primordia appear first at the 6th segment; the female, between the 7th (?) -14th proglottids. Testes, 50-70 in number, found in an irregular row in distal half of proglottid. Muscular cirrus sac contains the seminal vesicle and a long thin cirrus. The vagina opens just below the cirrus sac, and the two tend to form a genital papilla. Ovary usually indistinct, median (?). Douthitt reported it was 1.3 mm. in width. Uterus arises from female genital complex in fan-like fash-



Text-figures 10-17.

Abbreviations: c—cirrus sac. e—excretory duct. n—nerve fiber. o—ovary. p—pars prostatica. r—seminal receptacle. s—shell gland. t—testis. u—uterus. v—vitelline gland. va—vagina. vd—vas deferens. vs—seminal vesicle. All measurements are to a scale of 0.1 mm. All drawings are camera lucida.

10. Mature proglottid, *Schizotaenia americana*. 11. Mature proglottid, *Cittotaenia perplexa*. 12. Mature proglottid, *Cittotaenia variabilis*. 13. Mature proglottid, *Cittotaenia pectinata americana*. 14. Mature proglottid, *Cittotaenia denticulata*. 15. Mature proglottid, *Cittotaenia ctenoides*. 16. Mature proglottid, *Cittotaenia pectinata*. 17. Mature proglottid, *Andrya cuniculi*.

ion to fill median field. Ova range from 30-40  $\mu$  in material studied, but vary from 55-61  $\mu$ , according to Douthitt.

*Hosts*: Yellow-haired porcupine, *Erethizon epixanthes*; Canadian porcupine, *E. dorsatus*; and *Lepus* sp.

*Habitat*: Wyoming and New York.

### ***Cittotaenia perplexa* (Stiles, 1895).**

Stiles and Hassall, 1896.

(Text-figs. 3, 11).

This species was described by Stiles (1895) as *Ctenotaenia perplexa*, but was later transferred (Stiles and Hassall, 1896) to the genus *Cittotaenia* for reasons of priority. Later in 1896, Stiles published an inclusive diagnosis of the species.

In 1908, Hall described this same form as *Cittotaenia mosaica*, and later (1912) listed it from the intestine of *Sylvilagus nuttalli pinetis*, a cottontail rabbit of Colorado. The synonymy was pointed out by Douthitt (1915) who restudied Stiles' original specimens of *C. perplexa* (U. S. Nat. Mus., No. 1110). He found that Stiles' account was in error concerning the length of the cirrus sac and distribution of testes, and that the features which had been used to distinguish *C. mosaica* from *C. perplexa* were not significant differences.

Meggitt (1924) recognized *Cittotaenia perplexa* as a valid species with *C. mosaica* as a synonym. Baer (1927) reduced *C. perplexa* to synonymy with *Cittotaenia pectinata* (Goeze, 1782), which he considered to be exceedingly variable and widely distributed. Sprehn (1932) failed to mention either *C. perplexa* or *C. mosaica*.

In the present study, 26 incomplete specimens of *Cittotaenia perplexa* (Stiles, 1895) and *Cittotaenia mosaica* Hall, 1908, were loaned to the writer by Dr. M. C. Hall, U. S. Bureau of Animal Industry, U. S. Department of Agriculture. The specimens of *C. perplexa* bore the following numbers, U. S. Nat. Mus. Nos. 17226, 17246, and 17449. The specimens of *C. mosaica* were catalogued as U. S. Nat. Mus. Nos. 28429 and 24845. These included cotype material.

Of the fragments studied, the longest contained 150 proglottids and measured 70 mm. in length with a maximal width of 11 mm., the largest breadth yet reported. The greatest length reported previously (Hall, 1908) for *C. mosaica* was 100 mm. The scolex (Text-fig. 3) ranged from 0.32-0.45 mm. in width. The suckers were 0.11 mm. in diameter, which agrees with the measurement of Stiles. The scolex was not differentiated from a short and broad unsegmented neck, which measured from 0.30-0.35 mm. in length.

The genital organs were double and the pores opened anterolaterally. The female genital primordia appeared in the 10th proglottid and their ducts were first evident in the 16th. The male genital primordia first appeared about the 30th and their ducts in the 35th segment. The follicular ovary was well developed in the 70th segment, and disappeared in the 95th. This was correlated with the appearance of eggs in the uterus. This condition agreed with the observations of Hall and Douthitt. The ovary (Text-fig. 11) measured from 0.50-0.61 mm. in width. Douthitt reported a width of 0.85 mm. According to Hall, the yolk gland measured 0.20-0.23 in width, and the shell gland 0.074-0.092 mm. The seminal receptacle was rather large and situated within the longitudinal canals. The vagina was long and thin, opening below the cirrus sac. The ova ranged from 57-69  $\mu$  in diameter. Hall stated that they reached a maximum of 105  $\mu$ .

The testes, 120-125 in number, were in the distal half of the segment. In the younger proglottids, the testes were continuous from lateral canal to



lateral canal, while in more mature segments there was a definite median break in continuity of the chain. This was apparent both in Stiles' cotype material and in Hall's specimens of *C. mosaica*. The testes varied from 0.049-0.065 mm. in diameter. The maximal size recorded by Hall was 0.09 mm. The convoluted vas deferens proceeded from the region of the female glands to the long, narrow cirrus sac, which measured from 0.43-0.50 mm. in length. The maximal size recorded by Hall was 0.64 mm. In some of Stiles' material, Douthitt observed cirrus sacs as long as 0.55 mm.

The following diagnosis may be offered.

*Diagnosis: Cittotaenia perplexa* (Stiles, 1895) Stiles and Hassall, 1896. Mature specimens measure 3.8-10 cm. in length, and 11 mm. in maximal width. The scolex, 0.27-0.45 mm. in breadth, is not differentiated from a short, unsegmented neck region. Proglottids number over 150. Female genital primordia appear first in the 10th and their ducts in the 16th segment. Ovary well developed by the 70th segment; disappears at the 95th. Ovary, 0.50-0.85 mm. in width; ova 50 to 105  $\mu$  in diameter. Male genital primordia appear first in the 30th and their ducts in the 35th proglottid. Testes continuous from longitudinal canal to longitudinal canal in young proglottids, but divided into two groups in more mature ones. Testes 60-125 in number and 0.049-0.09 mm. in diameter. Cirrus sac 0.43-0.64 mm. long.

*Hosts: Sylvilagus nuttalli pinetis, Sylvilagus floridanus mallurus, and Sylvilagus floridanus alacer.*

*Habitat: Colorado, Maryland and Oklahoma.*

### ***Cittotaenia pectinata americana* Douthitt, 1915.**

(Text-figs. 6, 13, 19).

In 1896, Stiles declared that *Cittotaenia variabilis* (Stiles, 1895) is an American variant of *Cittotaenia pectinata* (Goeze, 1782) of Europe. Later discoveries have shown that *C. pectinata americana* of North America is much more closely related to *C. pectinata*. This American cestode was described by Lyman (1902) from *Lepus melanotis*, the common jackrabbit. Hall (1908) noted: "A hasty comparison of specimens of the European and American *C. pectinata* shows certain differences that should be determined as accidental or shown to be of specific or subspecific importance."

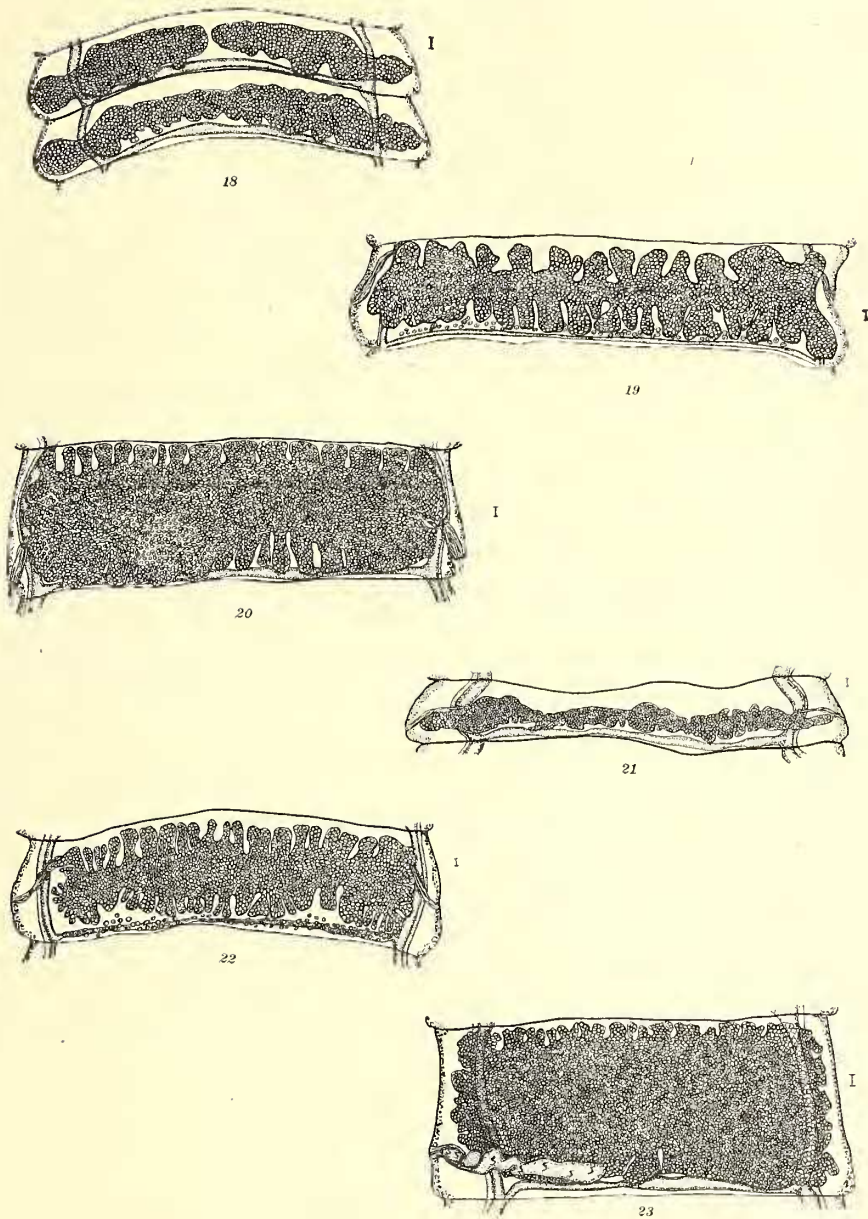
Later, Douthitt (1915) concluded that the American form "should be designated as a distinct variety to avoid confusion," and he proposed the name *C. pectinata americana*. This terminology was followed by Meggitt (1924), John (1926), Boughton (1932), and Rees (1933a).

Baer (1927) and Sprehn (1932) failed to recognize any distinctly American variety.

The author was fortunate in obtaining several paratype specimens of *C. pectinata americana* from Dr. R. V. Boughton. The original specimens of *C. pectinata americana*, which were described by Douthitt, were not available.

Ten almost complete specimens were studied. The longest, consisting of at least 360 proglottids, was 110 mm., and the broadest 7.5 mm. The scolex (Text-fig. 6), varying from 0.23-0.30 mm. in width, was set off only slightly from the neck, which measured 0.14-0.30 mm. in length. The suckers, ranging from 0.11-0.17 mm. in diameter, were shallow, situated at an angle, and very close together.

The female genital primordia were indicated first in the 5th-6th, and their ducts in the 6th-7th proglottids. The ovary (Text-fig. 13), averaging about 0.60 mm. in breadth, reached maturity between the 60th-90th segments, and disappeared abruptly between the 90th-145th proglottids (Text-fig. 19). The cirrus sac and, just below it, the vagina, opened into a shallow



Text-figures 18-23.

Abbreviations: c—cirrus sac, e—excretory duct, n—nerve fiber, o—ovary, p—pars prostatica, r—seminal receptacle, s—shell gland, t—testis, u—uterus, v—vitelline gland, va—vagina, vd—vas deferens, vs—seminal vesicle. All measurements are to a scale of 0.1 mm. All drawings are camera lucida.

- 18.** Gravid proglottid, *Cittotaenia variabilis*. **19.** Gravid proglottid, *Cittotaenia pectinata americana*. **20.** Gravid proglottid, *Cittotaenia denticulata*. **21.** Gravid proglottid, *Cittotaenia ctenoides*. **22.** Gravid proglottid, *Cittotaenia pectinata*. **23.** Gravid proglottid, *Andrya cuniculi*.

depression or atrium in the posterior half of the proglottid. The vagina continued mediad and very soon enlarged to form the seminal receptacle. The latter, thin-walled and irregular in outline, led to the ovarian complex. Ova ranged from 70-130  $\mu$  in diameter, with an average of 80  $\mu$ . The uterus was typically single.

The male genital primordia appeared first in the 37th-45th segments, and their ducts were visible one or two proglottids behind the primary condensation. The testes, about 125 per segment, 0.062-0.11 mm. in diameter, were situated in the posterior half of the proglottid, between the longitudinal excretory canals, posterior to the ovaries. The short vasa efferentia emptied into the vas deferens, which joined the convoluted seminal vesicle located median to the longitudinal excretory canal. The cirrus sac, 1.0-1.76 mm. in length, was well developed and extended mediad from the longitudinal excretory canal.

The following brief diagnosis is proposed.

**Diagnosis:** *Cittotaenia pectinata americana* Douthitt, 1915. Mature specimens may contain 360 proglottids, with a length of 220 mm. and a width of 7.5 mm. Scolex 0.23-0.30 mm. broad; neck 0.14-0.30 mm. long. Female genital primordia appear in the 5th or 6th and their ducts in the 6th or 7th segments. Ovary, about 0.6 mm. in breadth, reaches maturity in the 60th-90th and disappears between the 90th-145th segments. Ova 70-130  $\mu$  in diameter. The male genital primordia appear first between the 37th-45th proglottids, and their ducts in each instance one or two segments later. Testes, 112-125 per proglottid, measure from 0.062-0.11 mm. in diameter. They extend from one longitudinal excretory canal to the other, in the posterior half of the segment. Cirrus sac, 1-1.76 mm. long, extends mediad from the longitudinal excretory canal.

**Hosts:** *Lepus californicus melanotis* and *Lepus americanus*.

**Habitat:** Nebraska, Kansas and western Canada.

After a careful comparison of *C. pectinata americana*, of North America, and *C. pectinata*, of Europe, it was felt that the only justifiable allocation of these species is to retain the former as a variety of the latter. The chief difference between the two is that *C. pectinata* attains a length of 400 mm. with 190 proglottids, whereas *C. pectinata americana*, with a length of 220 mm., has more than 360 segments. This difference is distinctive and worth variety rank, considering that the specimens were from different hosts and from different continents. On the other hand, careful comparison affords no justification in separating them by more than variety status. The writer, therefore, agrees with Douthitt (1915) that the American representative of *C. pectinata* should be designated as a variety, *C. pectinata americana*.

### ***Cittotaenia variabilis* (Stiles, 1895).**

Stiles and Hassall, 1896.

(Text-figs. 2, 12, 18).

This species was described by Stiles in 1895 as *Ctenotaenia variabilis*. The next year, Stiles and Hassall transferred it to the present genus because of priority. Stiles felt proper classification of *C. variabilis* necessitated breaking up the species into three varieties: *C. variabilis variabilis*, *C. variabilis angusta*, and *C. variabilis imbricata*. These varieties were recognized by Lyman (1902) but not by Hall (1908), Douthitt (1915) or John (1926). Meggitt (1924) considered the varieties as synonyms of *C. variabilis*.

In the present study some of Stiles' original material of *C. variabilis* and 97 other specimens of this species were studied. Maximal length of



strobilia was 450 mm., with as many as 750 proglottids, and maximal width was 10.5 mm. The scolex, measuring 0.44-0.61 mm. in breadth, was typically set off from the neck, although in a few contracted specimens there was no line of demarcation (Text-fig. 2). The suckers, spherical in outline, varied from 0.16-0.28 mm. in diameter and averaged 0.21 mm. The neck measured from 0.26-0.84 mm. in length, with an average of 0.50 mm.

The female genital primordia appeared first between the 40th-50th and their ducts between the 95th-105th segments (Text-fig. 12). The follicular ovary measured from 0.48-0.71 mm. in width. The seminal receptacle, first differentiated at about the 160th segment, lay median to the longitudinal excretory canal, with its proximal end near the ovarian complex. Near its origin, the oviduct was joined by the duct from the seminal receptacle and the combined duct received shortly those from the yolk and shell glands. The tubular uterus then proceeded to the saccular uterus which was either single or double. The opening of the vagina was immediately below that of the cirrus sac. The ova ranged from 52-68  $\mu$  in diameter, with an average of 64  $\mu$  (Text-fig. 18).

The first appearance of the male genital primordia was thought to be in the vicinity of the 125th proglottid, although their ducts were not located definitely until the 175th. The testes were confined between the two ovaries in the distal half of the segment. They numbered between 60-135 and ranged from 0.053-0.071 mm. in diameter, with an average of 0.062 mm. The short vasa efferentia emptied into the vas deferens which proceeded to the highly convoluted seminal vesicle, lying for the most part median to the longitudinal excretory canal. Distally the vesicle joined the small cirrus sac (0.32-0.45 mm. long, averaging 0.38 mm.) lying lateral to the longitudinal excretory canal. The cirrus sac, testes, ovary, and female ducts degenerate in ripe proglottids.

From the above data the following diagnosis may be given.

*Diagnosis: Cittotaenia variabilis* (Stiles, 1895), Stiles and Hassall, 1896. Mature specimens with as many as 750 proglottids attain a maximal length of 450 mm. and a maximal breadth of 10.5 mm. Scolex 0.44-0.61 mm. in width; may or may not be set off from the neck. Suckers 0.16-0.28 mm. in diameter, average 0.21 mm. Neck well defined; length 0.26-0.84 mm., average 0.50 mm. Female genital primordia appear between the 40th-50th and their ducts between the 95th-105th proglottids. Ovary measures 0.43-0.71 mm. in width, with an average of 0.58 mm. Ova 52-68  $\mu$  in diameter, with an average of 64  $\mu$ . Male genital primordia appear about the 125th proglottid and their ducts at the 175th. Testes (60-135) in the distal half of the proglottid between the two ovaries; diameter 0.053-0.071 mm. Cirrus sac small, 0.32-0.45 mm. long, lateral to longitudinal excretory canal.

*Hosts: Sylvilagus floridanus mallurus, S. floridanus alacer and S. palustris.*

*Habitat:* New York, Maryland, Kansas and Pennsylvania.

## 6. CORRELATION OF HOST-PARASITE RELATIONS.

In the present survey, 179 cottontail rabbits were examined. For identification the systematic arrangement of Nelson (1909) was employed. *Sylvilagus floridanus mallurus* was obtained from New York and Pennsylvania, and *S. floridanus alacer* from Kansas. *Cittotaenia variabilis* (Stiles, 1895) was the only cestode recovered. The parasites were usually found near the middle of the small intestine, although more anteriorly in a few cases.

Tables I and II give the data on infection in the rabbits studied.

TABLE I. *Sylvilagus floridanus mallurus*.

Locality.	No. Examined.	No. Infected.	% Infected.
Lake Mahopac, N. Y.	3	2	66 $\frac{2}{3}$
Pinebush, N. Y.	3	1	33 $\frac{1}{3}$
Carmel, N. Y.	1	1	100
New York, N. Y.	2	1	50
Northern New York.	7	6	85.9
Boylesville, Pa.	7	2	28.5
Total.	23	13	56.5

TABLE II. *Sylvilagus floridanus alacer*.

Locality.	No. Examined.	No. Infected.	% Infected.
Wichita, Kan. 1932	28	19	67.8
Wichita, Kan. 1933	50	19	38
Wichita, Kan. 1934	78	32	41
Total.	156	70	44.8

*Cittotaenia pectinata americana* (Douthitt, 1915) is found only in hares, namely, *Lepus californicus melanotis* Mearns and *Lepus americanus* Erxleben. *Cittotaenia perplexa* (Stiles, 1895) and *C. variabilis* (Stiles, 1895) are found only in cottontail rabbits. Both species are present in *Sylvilagus floridanus mallurus* (Thomas) and *Sylvilagus floridanus alacer* (Bangs), while only *Cittotaenia perplexa* has been found in *Sylvilagus nuttalli pinetis* (Allen) and only *C. variabilis* in *Sylvilagus palustris* (Bachman).

#### 7. ANOPLOCEPHALINE CESTODES FROM EUROPEAN HARES AND RABBITS.

##### ***Cittotaenia denticulata* (Rudolphi, 1804).**

Stiles and Hassall, 1896.

(Text-figs. 4, 8, 14, 20).

*C. denticulata*, type species of *Cittotaenia*, was first described by Rudolphi as *Taenia denticulata*. The original description was expanded in later papers (Rudolphi, 1805, 1810). The same species was subsequently described by Baird (1853) as *Taenia goezei*.

The next important work is that of Riehm (1881a), who described this worm first as *Cittotaenia latissima*, gen. nov., sp., nov., and then as a species of *Dipylidium*. *Dipylidium latissima* was transferred to the genus *Taenia* by Neumann in 1888.

*Taenia goezei* Baird was reduced to synonymy with *D. latissima* Riehm by Blanchard (1891) on reexamination of Baird's original material.

Riehm's *D. latissima* was placed in the genus *Ctenotaenia* by Railliet in 1893.

Stiles and Hassall (1896), upon study of the original specimens of Rudolphi's *Taenia denticulata*, Baird's *Taenia goezei*, and Riehm's *Dipu-*

*lidium latissima*, declared that they were all the same species which they recognized as *Cittotaenia denticulata*. Later descriptions of *C. denticulata* include those of Stiles (1896), John (1926), Baer (1927) and Sprehn (1932).

In the present study, 19 specimens of *Cittotaenia denticulata* were examined. They ranged from minute, immature forms to large, fully matured cestodes with as many as 260 proglottids. They measured 0.149-260 mm. in length and 8.5 mm. in maximal breadth (Text-fig. 4). The solices of the immature forms (worms 0.149-10.5 mm. in length) ranged from 0.10-0.50 mm. in width; those of mature worms (21-260 mm. in length) varied from 0.57-0.76 mm. in breadth. The scolex appeared to be rectangular in cross section. There was a short broad neck, not previously reported, which measured from 0.21-0.92 mm., depending on the degree of contraction. The suckers ranged from 0.23-0.30 mm. in diameter, averaging 0.27 mm. The sucker size was in close agreement with that found by other workers.

The female genital primordia were first seen between the 10th-15th, and their ducts between the 17th-40th proglottids. The ovarian follicles were not well developed until the 80th-100th proglottid (Text-fig. 14). The follicles continued to increase in size and then suddenly disappeared between the 135th-175th segments. The ovary measured from 0.32-1.42 mm. in width and averaged 0.97 mm. The disappearance of the ovary is correlated with the presence of eggs in the uterus (Text-fig. 20). The ovaries were found in the posterior two-thirds of the proglottid and just median of the longitudinal excretory canals. The oviduct originated about the middle of the ovarian mass, and after a short distance was joined by the short duct from the bulbous seminal receptacle. The combined duct then passed to the shell gland, where it was joined by the vitelline duct. The tubular uterus then proceeded anteriorly to the saccular uterus. The ova measured from 46-75  $\mu$  in diameter and averaged 61  $\mu$  (Text-fig. 8).

The male genital primordia were first seen between the 35th-60th, their ducts, between the 36th-70th proglottids. The testes increased in number very rapidly after the first appearance of their primordia. The follicles extended between the longitudinal excretory canals and were scattered between the anterior and posterior limits of the proglottid. The testes totaled between 225 and 250, a number very much greater than that previously recorded. Baer and Sprehn reported that there were 100 testes. Stiles and John merely stated that they were numerous. However, Stiles (1896) gave a drawing of one-half of a mature segment of *C. denticulata*. The writer counted the testes represented in that half segment and found that there were 124. Since Stiles worked on the original material of Rudolphi, Baird and Riehm, and his drawing was apparently taken from that material, it seems safe to assume that the number of testes is nearer 225-250 than 100. The vasa efferentia emptied on either side of the proglottid into a vas deferens which proceeded to the cirrus sac containing the seminal vesicle and a large cirrus. The cirrus sac measured from 0.50-0.97 mm. and averaged 0.77 mm. in length, which was within the range given by other workers. The testes ranged from 0.041-0.12 mm. and averaged 0.073 mm. in diameter. This range is much smaller than that given by other authors, but it is inclusive of some of the higher values found by others. The testes tend to disappear in ripe proglottids.

From the above description the following diagnosis may be drawn.

**Diagnosis:** *Cittotaenia denticulata* (Rudolphi, 1804) Stiles and Hassall, 1896. Type of the genus. Mature specimens range 20-800 mm. in length, with as many as 300 proglottids, and from 8-15 mm. in maximal breadth. Scolex 0.57-1.18 mm. wide; 0.43-1 mm. long. Suckers 0.2-0.3 mm. in diameter. The genital primordia appear early. Those of the female system are found between the 10th-15th proglottids, and their ducts between the 17th-40th proglottids. Ovary, 0.32-1.42 mm. in width, becomes well devel-



oped at about the 84th-100th and disappears about the 135th-170th segment. Male genital primordia appear first between the 35th-60th and their ducts between the 36th-70th segments. Testes range from 225-250 in number in mature proglottids, and vary between 0.041-0.12 mm. in diameter. Cirrus sac measures from 0.50-1.12 mm. in length and 0.26-0.3 mm. in width. Ova measure 46-75  $\mu$  in diameter.

*Host: Oryctolagus cuniculus.*

*Habitat: Europe.*

***Cittotaenia ctenoides* (Riehm, 1881).**

Stiles and Hassall, 1896.

(Text-figs. 9, 15, 21).

*Cittotaenia ctenoides* was first described as *Dipylidium leuckarti* by Riehm in 1881. Later it was transferred to the genus *Taenia* by Neumann (1888) and in 1892 it was replaced in the genus *Dipylidium* by the same author.

In 1890, Railliet changed the specific name from *Taenia leuckarti* to *Taenia ctenoides*. R. Blanchard (1891) placed *Dipylidium leuckarti* Riehm in the genus *Moniezia*. Railliet (1893) erected the genus *Ctenotaenia* and placed the species *Taenia ctenoides* in it. The synonymy of this genus with *Cittotaenia* was pointed out by Stiles and Hassall (1896). Later accounts of this species were given by Stiles (1896) (who studied Riehm's type specimens and others from Blanchard's collection), by Baer (1927), and by Sprehn (1932).

The writer examined 100 specimens of *C. ctenoides*, ranging from 6-460 mm. in length and from 1-10.5 mm. in width. The maximal length found was less than that previously reported, while the maximal width was somewhat greater. The scolex was small, although wider than the neck region and proximal proglottids. It measured 0.32-0.48 mm. in width (Text-fig. 9). This range is smaller than that reported by Stiles, Baer or Sprehn, although the higher value was in agreement. The suckers measured 0.12-0.25 mm. in diameter, with an average of 0.16 mm. There was a short broad neck which varied from 0.25-0.42 mm. and averaged 0.32 mm. in length. The neck was not measured by Stiles, and Baer and Sprehn did not mention it. The proglottids reached a number greater than 560. Stiles reported a maximum of 750 proglottids. The original, terminal 10-15 proglottids, when present, were sterile.

The female genital primordia appeared in the first few proglottids, but their ducts were not distinct until the 45th-50th segments. A well developed follicular ovary was first seen in the 130th-160th segments (Text-fig. 15). The ovary then continued to develop and later suddenly disappeared between the 183rd-232nd proglottids. This disappearance of the ovary was correlated with the presence of eggs in the uterus. The ovary measured from 0.40-0.88 mm. in width and averaged 0.61 mm. The oviduct arose posteriorly from the ovary and was joined almost immediately by the duct from the seminal receptacle. The convoluted oviduct proceeded posteriad to join the rather long vitelline duct, in the shell gland mass. The tubular uterus then proceeded antieriad and slightly laterad for a short distance, where it enlarged into the saccular uterus (Text-fig. 21). The ova ranged from 62-69  $\mu$ , and averaged 66  $\mu$  in diameter. This figure is slightly higher than those given by Stiles, Baer, and Sprehn. The seminal receptacle was not clearly delimited. The vagina opened to the exterior immediately below the opening of the cirrus sac. It proceeded as a small tube mediad and slightly posteriad for a short distance and then expanded to form the seminal receptacle. The seminal receptacle gradually narrowed to a duct which proceeded antieriad and mediad to join the oviduct.

The male genital primordia appeared first between the 85th-100th segments, and the ducts were found a few proglottids farther back. The testes were divided into two groups, one on either side of the proglottid, posterior to the ovaries and median to the longitudinal excretory canal. The testes numbered from 35-75 in each group, and the two groups contained approximately the same number of follicles. The number of testes found was less than that given previously by other workers. The testes varied from 0.046-0.081 mm. and averaged 0.056 mm. in diameter. The short vasa efferentia joined the vas deferens which proceeded antieriad and laterad to the cirrus sac. The small lateral cirrus sac, containing the seminal vesicle and a well developed cirrus, varied from 0.16-0.25 mm. in length, with an average of 0.23 mm. These measurements are slightly higher than those reported by Stiles, Baer and Sprehn.

The following brief diagnosis is suggested.

*Diagnosis: Cittotaenia ctenoides* (Railliet, 1890) Stiles and Hassall, 1896. Strobila, of 500-750 proglottids, may attain a length of 800 mm. and a maximal breadth of 10.5 mm. Scolex, 0.32-0.50 mm. wide, is broader than the neck and proximal proglottids. Suckers 0.12-0.25 mm. in diameter. Female reproductive primordia appear very soon after segmentation begins; their ducts at 45th-50th segments. Ovary, 0.40-0.88 mm. wide, develops between 130th-160th, and disappears about 183rd-232nd proglottids. Ova 62-69  $\mu$  in diameter. Male reproductive primordia appear first at 85th-100th segments and their ducts very soon thereafter. Testes, 0.046-0.081 mm. in diameter, arranged in two groups (35-80 in each). Cirrus sac 0.16-0.25 mm. long and 0.138-0.23 mm. wide.

*Hosts: Oryctolagus cuniculus* and *Oryctolagus cuniculus domesticus*.

*Habitat:* Europe.

### ***Cittotaenia pectinata* (Goeze, 1782).**

Stiles and Hassall, 1896.

(Text-figs. 7, 16, 22).

*Cittotaenia pectinata* was first described by Goeze (1782) as *Taenia pectinata* from hares and wild rabbits. His description was vague and inadequate, and pertained to material of more than one species.

Zeder (1800) transferred the species to the genus *Alyselminthes*. His description was supposed to cover *T. pectinata*, but subsequent workers feel he actually studied *Andrya rhopalocephala*. In 1803, Zeder placed *T. pectinata* in the genus *Halysis*.

Rudolphi (1810), Bremser (1824), and Diesing (1850) studied *T. pectinata* but their characterizations for this species were broad enough to include several species.

Riehm (1881) was the first to study the species in detail. After rectifying previous errors, he placed *T. pectinata* in the genus *Dipylidium*. In 1891, Blanchard reported this species at Briançon.

The species was included in the genus *Ctenotaenia* by Railliet in 1893, but Stiles and Hassall (1896) transferred it to the genus *Cittotaenia*.

Stiles (1896) obtained some of Riehm's original material and elaborated Riehm's diagnosis. Stiles summarized the works of previous authors and gave a more complete description.

Douthitt (1915) stated that *C. pectinata* was found only in Europe. This allocation was followed by Meggitt (1924), John (1926), and Rees (1933a).

Baer (1927) claimed that *C. pectinata* was very extensively distributed. He considered all American representatives of the genus *Cittotaenia* in

rabbits to be *Cittotaenia pectinata*. Sprehn (1932) followed Baer in his consideration of this species.

The author studied 29 specimens of *Cittotaenia pectinata* (Goeze, 1782), varying from 0.97-84 mm. in length and from 0.17-8 mm. in maximal breadth. Stiles reported a greater length than this, 400 mm. Blanchard found a width of 10 mm. The small scolex was rarely wider than the proglottids immediately following it. The scolex measured from 0.20-0.35 mm. in width, with an average of 0.28 mm. (Text-fig. 7). The suckers were set at an angle and were very close together. They ranged from 0.071-0.15 mm. in diameter, with an average of 0.12 mm.. The neck region measured from 0.10-0.35 mm. in length and averaged 0.20 mm. The proglottids were always much broader than long and numbered as high as 190. The terminal proglottids were found to be sterile, an anoplocephaline characteristic.

The female genital primordia appeared by the 8th proglottid, while their canals were found between the 10th-15th segments. The ovaries, measured only in mature proglottids, ranged from 0.21-0.67 mm. in width, with an average of 0.48 mm. (Text-fig. 16). The ovary developed steadily from the primordial stage to that found in fully mature proglottids, and then disappeared rather abruptly between the 75th-150th proglottids. The follicles of the ovary were not well developed until the 45th-60th proglottids. The oviduct arose medially from within the mass of the ovary and then proceeded anteriorly. Within a short distance it joined the duct from the seminal receptacle. The oviduct then proceeded posteriorly and soon met the ducts from the vitelline and shell glands. The convoluted tubular uterus passed anteriorly to meet the sacculus uterinus near its posterior limits. The uterus was either double or the two uteri became confluent in the middle of the segment to form a single continuous one. The former type was the one commonly encountered (Text-fig. 22). The ova ranged from 62-67  $\mu$  in diameter and averaged 65  $\mu$ .

The male and female reproductive systems opened to the exterior by a common genital pore, or by two pores which were situated exceedingly close together. The vagina opened to the exterior below the cirrus sac, or into the cirrus sac just at its opening to the outside. The latter condition seemed the more common. The vagina soon expanded into the seminal receptacle, a large, thin-walled structure, which was closely applied to the cirrus sac and seminal vesicle. Medially, the seminal receptacle became a duct that led to the oviduct.

The male genital primordia first appeared between the 25th-45th proglottids, or 1.4-5.6 mm. from the anterior end, and the male ducts between the 27th-47th segments. The testes, in mature proglottids, ranged from 80-160 in number, and averaged 130. They lay along the posterior border of the proglottid, between the longitudinal excretory canals, below the distal half of the ovary. They measured from 0.043-0.077 mm. in diameter, with an average of 0.06 mm. The vasa efferentia emptied shortly into the vas deferens, which proceeded to join the seminal vesicle near the anterior end of the proglottid. The seminal vesicle was much convoluted, and medial to the longitudinal excretory canal. The glandular cells of the pars prostatica surrounded the seminal vesicle. The cirrus sac was thick-walled, muscular and contained a well developed cirrus. The cirrus sac ranged from 0.36-1.03 mm. in length and averaged 0.69 mm. The cirrus sac and the seminal vesicle lay at a slight angle, and the genital pores (one on either side of the segment) were situated in the posterior half of the proglottid.

From the literature and the study of both whole mounts and sections, the specific diagnosis, given below, has been derived.

*Diagnosis: Cittotaenia pectinata* (Goeze, 1782) Stiles and Hassall, 1896. Mature specimens 400 mm. long and 10 mm. wide. Scolex 0.20-0.35 mm. wide. Broad, short neck measures 0.10-0.15 mm. in diameter. Female



genital primordia appear by 8th segment, their ducts, by 10th-15th segment. Ovary, 0.21-0.67 mm. wide, disappears between 75th-150th segments. Ova 54-90  $\mu$  in diameter. Male genital primordia appear first between the 25th-45th, their ducts between 27th-47th segments. Testes, 80-160 in number, 0.043-0.077 mm. in diameter, lying in distal half of proglottid, extend from one longitudinal excretory canal to other. Cirrus sac, 0.36-1.03 mm. in length, extends mediad beyond the longitudinal excretory canal.

*Hosts: Oryctolagus cuniculus, Lepus europaeus, Lepus timidus, Lepus variabilis and Marmota marmota.*

*Habitat: Asia and Europe (Germany, France and England).*

### ***Andrya cuniculi* (R. Blanchard, 1891).**

Railliet, 1893.

(Text-figs. 5, 17, 23).

*Andrya cuniculi*, first described by Riehm (1881) as *Taenia rhopalioccephala*, was placed in the genus *Anoplocephala* in 1891 by Blanchard when he changed the specific name to *cuniculi*. In regard to this transfer, he stated:

"*A. cuniculi* R. Blanchard, 1891 (*Taenia pectinata* Göze, 1782, pro parte; *T. rhopalioccephala* Riehm, 1881).—Chez le Lapin de garenne. Le nom proposé par Riehm ne peut pas être conservé, en raison de son identité avec le nom de *Taenia rhopalocephala*; ce dernier seul est valable: il a la priorité, puisque la ver auquel il s'applique est décrit par Riehm quelques pages avant le *Taenia rhopalioccephala* (3), et d'ailleurs est le seul dont le nom soit correctment formé."

Railliet (1893) erected the genus *Andrya* to contain *A. rhopalocephala* and *A. cuniculi*. Stiles (1896) restudied Riehm's original material and gave his own characterization of this species. He stated that he has never recovered this parasite from rabbits in North America. Douthitt (1915) and Meggitt (1924) both recognized this species as valid, but gave no further characterization of it. Baer (1927) and Sprehn (1932) studied this form, but gave nothing new in their monographs.

The present writer studied 38 specimens of *Andrya cuniculi*. They ranged from 13-325 mm. in length. The maximal breadth obtained was 3.5 mm. These measurements were only about one-third the maximum length and width previously reported. The scolex was large, varying from 0.40-0.67 mm. in diameter. It was definitely set off from a well differentiated neck (Text-fig. 5). The latter measured from 0.80-1.42 mm. in length. The large suckers ranged from 0.16-0.30 mm. in diameter, with an average of 0.25 mm. The immature segments were much broader than long, while the mature proglottids tended toward a quadrate condition. The segments numbered as many as 500. Stiles (1896) reported them to be as many as 800. He undoubtedly had more mature specimens than were studied in this survey. The original 2-7 terminal proglottids were sterile.

The reproductive organs were single. Their genital openings were irregularly alternate on right and left lateral margins (Text-fig. 17), but opened more often on one side than on the other, as previously observed by Stiles. The female genital primordia appeared first about the 5th-10th proglottids, and their ducts between the 95th-110th segments. The ovarian follicles were not well developed until the 225th-275th proglottids. The ovary measured from 0.43-0.50 mm. in width, and was median or on the poral side of the segment. The vagina was distal to the cirrus sac and its openings. It extended mediad to the longitudinal excretory canal and enlarged into the seminal receptacle. The latter extended to the ovarian mass, where it joined the oviduct. The latter duct, upon uniting with the yolk and shell glands, gave rise to the uterus (Text-fig. 23). Stiles (1896) stated that the

latter was characteristically a network structure. The ova measured from 49-57  $\mu$  in diameter, which was within the range given by Stiles (1896).

The male genital primordia were first evident about the 45th segment, and their ducts at the 110th segment. The testes extended between the two longitudinal excretory canals, and the anterior and posterior limits of the proglottid. They practically surrounded the ovary, although they were more predominantly distributed on the side opposite the genital pore. They numbered between 70-90 and varied from 0.049-0.065 mm. in diameter. The vasa efferentia very soon joined the vas deferens. Just before the latter emptied into the cirrus sac, it united with the pars prostatica. The cirrus sac was club-shaped, extended mediad of the longitudinal excretory canal and contained a definite seminal vesicle. The cirrus sac measured from 0.27-0.43 mm. in length. This range is lower than that given by Stiles, but may be explained by the fact that the specimens used in this study were not as mature (long) as those used by Stiles. There seemed to be a tendency for the formation of a genital papilla, which contained both male and female genital openings.

Summarizing the above surveys, the following diagnosis is derived.

*Diagnosis:* *Andrya cuniculi* (R. Blanchard, 1891) Railliet, 1893. Mature specimens, with as many as 800 segments, 1,000 mm. long and 8 mm. wide. Scolex 0.4-0.67 mm. wide. Well differentiated neck, 0.80-1.42 mm. long. Suckers 0.16-0.30 mm. in diameter, with an average of 0.25 mm. Female genital primordia appear first in 5th-10th and their ducts in 95th-110th proglottids. Ovary 0.43-0.50 mm. wide. Ova 49-57  $\mu$  in diameter. Male genital primordia appear first in about 45th proglottid and their ducts in 110th. Testes in median field, 70-90 per segment, varying from 0.049-0.065 mm. in diameter. Cirrus sac, 0.27-0.8 mm. long, extends mediad of the longitudinal excretory canal.

*Hosts:* *Lepus timidus* and *Oryctolagus cuniculus*.

*Habitat:* Europe.

## 8. COMPARISON OF EUROPEAN AND AMERICAN ANOPOLOCEPHALIDAE OF RABBITS.

The members of the Anoplocephalidae from North American rabbits show constant differences from those of European rabbits.

*Schizotaenia americana* (Stiles, 1895) and *Andrya cuniculi* (R. Blanchard, 1891) are immediately distinguished from the several species of rabbit cestodes of the genus *Cittotaenia* by the fact that they possess only one set of genital organs to a proglottid. *S. americana* differs from *A. cuniculi* in regularity of alternation of the genital pores, length and width of body, lack of neck, number of proglottids, size of ovary, first appearance of male genital primordia and ducts, and number of testes.

*Cittotaenia denticulata* (Rudolphi, 1804) differs from *C. ctenoides* (Railliet, 1890) in size of scolex, number of proglottids, earliest appearance of female genital ducts, position of ovarian maturity and disappearance, first indication of male genital primordia and ducts, number of testes and their distribution, and size of cirrus sac. It is unlike *C. pectinata* (Goeze, 1782) in maximal length, number of proglottids, first appearance of female genital primordia and ducts, position of ovarian maturity, number and distribution of testes, and location of cirrus sac. *C. perplexa* (Stiles, 1895) is different from *C. denticulata* in maximal length, size of scolex, diameter of sucker, number of proglottids, appearance of ovarian follicles, number and distribution of testes, and location of cirrus sac. *C. denticulata* is dissimilar to *C. pectinata americana* Douthitt, 1915, in maximal length, maximal width, size of scolex, size of sucker, number and distribution of testes, and position of cirrus sac. *C. denticulata* is unlike *C. variabilis* (Stiles, 1895) in maximal length and width, size of neck, number of

proglottids, position of genital primordia and ducts of both male and female reproductive systems, number and distribution of testes, and size of cirrus sac.

*C. ctenoides* is unlike *C. denticulata* in scolex size, sucker diameter, proglottid number, first indication of female reproductive ducts, site of ovarian maturity and disappearance, earliest appearance of male genital primordia and ducts, number and distribution of testes, and size of cirrus sac. *C. ctenoides* differs from *C. pectinata* in maximal length, number of proglottids, first indication of female ducts, ovarian maturity and disappearance, location of male genital primordia and ducts, distribution of testes, and length and position of cirrus sac. *C. perplexa* is distinct from *C. ctenoides* in maximal length, size of suckers, number of proglottids, site of female genital duct appearance, maturity and disappearance of ovary, first appearance of male genital primordia and ducts, and size of cirrus sac. *C. ctenoides* is dissimilar to *C. pectinata americana* in maximal length and width, size of scolex, number of proglottids, first indications of female genital primordia, first appearance of male genital primordia and ducts, maturity and disappearance of ovary, distribution and size of testes, and position of cirrus sac. *C. variabilis* is different from *C. ctenoides* in maximal length, appearance of genital primordia and ducts of both male and female reproductive systems, distribution of testes, and length and position of cirrus sac.

*C. pectinata* differs from *C. denticulata* in maximal length, scolex width, sucker diameter, number of proglottids, location of ovarian maturity, testes number and distribution, and cirrus sac size. *C. pectinata* is unlike *C. ctenoides* in maximal size, number of proglottids, time of appearance of genital primordia and of ducts of both male and female reproductive systems, maturity and disintegration of ovary, distribution of testes and size and location of cirrus sac. The comparison of *C. pectinata* with the next three American species is of especial interest, since Baer (1927) and Sprehn (1932) considered them identical with *C. pectinata*. The latter is distinct from *C. perplexa* in maximal length, first appearance of female genital primordia and their ducts, site of first ovarian follicular development, and distribution of testes in mature proglottids. *C. pectinata* has a variant in *C. pectinata americana* but differs from it in maximal length and breadth and number of proglottids. *C. pectinata* is unlike *C. variabilis* in size of scolex, length of neck, size of suckers, number of proglottids, appearance of primordia and ducts of both male and female reproductive systems, distribution of testes, and length and location of cirrus sac.

*C. perplexa* differs from *C. denticulata* in maximal length, scolex width, sucker diameter, proglottid count, site of earliest complete follicular development and disintegration, testes number and distribution, and cirrus sac location. *C. perplexa* is different from *C. ctenoides* in maximal length, sucker size, number of proglottids, first appearance of female genital canals, location of ovarian follicular maturity and disappearance, earliest appearance of male genital primordia and ducts, and cirrus sac position. *C. perplexa* is unlike *C. pectinata* in maximal length, earliest appearance of female genital primordia and their ducts, location of first ovarian follicular development, and distribution of testes in mature segments. *C. perplexa* is dissimilar to *C. pectinata americana* in maximal length and breadth, maximal number of proglottids, earliest appearance of female ducts, first appearance of the male genital primordia and ducts, testes distribution, and cirrus sac characteristics. *C. perplexa* is distinct from *C. variabilis* in maximal length, scolex size, length of neck, sucker size, number of proglottids, place of appearance of genital primordia and ducts of both male and female reproductive systems, distribution of testes, and size and location of cirrus sac.

*C. pectinata americana* is unlike *C. denticulata* in maximal length, size of scolex and suckers, number of proglottids, number and distribution of



testes, and cirrus sac characteristics. *C. pectinata americana* differs from *C. ctenoides* in maximal length and breadth, number of proglottids, first appearance of female genital ducts, first appearance of male genital primordia and ducts, site of ovarian maturity and disappearance, testes distribution, and cirrus sac size and position. *C. pectinata* is different from *C. pectinata americana*, its variety, in maximal length and breadth, and number of proglottids. *C. pectinata americana* is unlike *C. perplexa* in maximal length and breadth, number of proglottids, first appearance of genital primordia and ducts of both male and female reproductive systems, testes distribution, and cirrus sac size. *C. pectinata americana* is distinct from *C. variabilis* in maximal length and breadth, size of scolex, number of proglottids, first appearance of genital primordia and of ducts of both male and female reproductive systems, testes distribution, and cirrus sac size and position.

*C. variabilis* is divergent from *C. denticulata* in maximal length, length of neck, number of proglottids, appearance of genital primordia and of ducts of both male and female reproductive systems, number and distribution of testes, and size of cirrus sac. *C. ctenoides* is distinct from *C. variabilis* in maximal length, length of neck, earliest appearance of male and female genital primordia and ducts, testes, distribution, and cirrus sac size. *C. variabilis* is dissimilar to *C. pectinata* in scolex width, length of neck, sucker size, segment count, appearance of male and female genital primordia and ducts, testes distribution, and cirrus sac length. *C. variabilis* is unlike *C. perplexa* in maximal length, size of scolex, length of neck, size of suckers, site of appearance of genital primordia and ducts of both male and female reproductive systems, distribution of testes, and length of position of cirrus sac. *C. variabilis* is unlike *C. pectinata americana* in maximal length and breadth, width of scolex, number of proglottids, earliest appearance of genital primordia and ducts of both male and female reproductive systems, distribution of testes, and size and position of cirrus sac.

#### 9. KEY TO SPECIES.

Contrary to the findings of Baer (1927) and Sprehn (1932), the anoplocephaline species of leporine cestodes in North America and Europe are separate and distinct. Representatives of three genera of the Anoplocephalidae have been found in hares and rabbits. The genus *Schizotaenia* Janicki, 1906, is represented by *S. americana* (Stiles, 1895) and this species is found only in North America. The genus *Andrya* Railliet, 1893, is represented by *A. cuniculi* (R. Blanchard, 1891) and is found only in Europe. Finally the genus *Cittotaenia* Riehm, 1881, has members in both North America and Europe and contains six species. They include *C. denticulata* (Rudolphi, 1804), *C. ctenoides* (Railliet, 1890), and *C. pectinata* (Goeze, 1782), all found in Europe, and *C. perplexa* (Stiles, 1895), *C. variabilis* (Stiles, 1895), and *C. pectinata americana* Douthitt, 1915, all found in North America. *C. pectinata* and *C. pectinata americana* are parasitic principally in hares (*Lepus*), whereas the other species of *Cittotaenia* occur chiefly in rabbits (*Oryctolagus* and *Sylvilagus*).

The Anoplocephalidae of rabbits may be distinguished by the following key:

1. (2) Two sets of reproductive organs to a segment. (5)
2. (1) One set of reproductive organs to a segment. (3)
3. (4) Genital pores alternating regularly to right and left lateral margins.  
*Schizotaenia americana*.
4. (3) Genital pores alternating irregularly to right and left lateral margins.  
*Andrya cuniculi*.
5. (6) Cirrus sac extending medial of longitudinal excretory canal. (10).
6. (5) Cirrus sac lying lateral of longitudinal excretory canal. (7).

7. (8) Maximal number of proglottids—300; first appearance of female genital ducts between 17th-40th proglottids; earliest indication of male genital primordia and ducts from the 35th-60th and 36th-70th proglottids, respectively. *Cittotaenia denticulata*.
8. (9) Maximal number of proglottids—750; first appearance of female genital ducts between 45th-50th segments; first indication of male genital primordia and ducts between 75th-100th and 76th-105th proglottids, respectively. *Cittotaenia ctenoides*.
9. (7) Maximal number of proglottids—750; female ducts indicated first between the 95th-105th segments; male genital primordia and ducts originating at 125th-175th proglottids, respectively; well defined neck present. *Cittotaenia variabilis*.
10. (11) Cirrus sac just barely crossing longitudinal excretory canal, and with a maximal length of 0.64 mm.; maximal body length, 100 mm. *Cittotaenia perplexa*.
11. (12) Cirrus sac extending considerably mediad of excretory canal, and with a maximal length of 1.03 mm.; proglottids up to 190; maximal body length, 400 mm. *Cittotaenia pectinata*.
12. (10) Cirrus sac extending much mediad of longitudinal excretory canal; cirrus sac with a maximal length of 1.8 mm.; proglottid number, more than 360; maximal body length, 220 mm. *Cittotaenia pectinata americana*.

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